PAPERS.

48. The One-sided Reduction of the Ovaries and Oviducts in the Amniota, with Remarks on Mammalian Evolution. By Hans Gadow, M.A., Ph.D., F.R.S., F.Z.S.

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Index.

Sanguine morphologists reckon that it takes about ten years for their discoveries to find their way into a text-book. It takes a generation to eradicate erroneous statements, especially generalisations, out of such books, since most of them are repeated from others without consultation of the immense host of original papers. And it is apparently hopeless to expect the enthusiast or amateur to appreciate the difference between a generalising text-book of comparative anatomy and a zootomical account. It means progress for a branch of science if we can inscribe upon its statute-book a few lines of true generalisation, which, if there be no hedging, require no longer any concrete examples to be mentioned. If only partial generalisations are possible, of course the exceptions are to be recorded and every new case is welcome, until their accumulation in turn permits of being summarised. Then let there be drawn a line, and let the discoverer of further cases keep his peace unless he has something new to say.

The condition of the bird's ovaries and oviducts is a case in point. The main facts have by now become ancient history and general knowledge to the zoologist, so ancient that the original workers have been forgotten, as much as the name of the originator of the term morphology.

That the ovaries and ducts of birds are one-sided was probably known since time immemorial. Perrault * described and figured them in the Ostrich without further comment. In the year 1810 Wolf mentioned that he had usually found two ovaries in the Sparrow-hawk, a fact duly incorporated by Tiedemann † in his excellent work, which reveals him as a zoologist far ahead of his time. Next, Spangenberg ‡ figured the right ovary in a Duck. Barkow § described the occurrence of right-sided rudiments of the female generative apparatus in various other birds. Emmert || observed equally large right and left ovaries in the Sparrow-

* Perrault: Mémoires pour servir à l'histoire naturelle. Amsterdam, 1736.

† Tiedemann: Anatomie und Naturgeschichte der Vögel. 1810.

‡ Spangenberg: Disquisitiones circa partes genitales fœmineas Avium. Gottingæ, 1813, 4to.

§ Barkow: Von der Kloake verschiedener Vögel. Meckel's Archiv f. Anat. u. Phys., 1829.

|| Emmert: Reil u. Authenriet's Archiv.

hawk and some other Accipitres. When Nitzsch made his anatomical contributions to Naumann's 'Naturgeschichte' he knew already of quite a number of cases of double ovaries. R. Wagner* added to them in his Lehrbuch, and still more in his Beiträge. He described the cases of double ovaries accompanied by double ducts; he knew that vestigial ducts are much rarer than ovaries, and was well aware of the fact that even in Accipitres with double ovaries there may be no traces of a second duct, etc. Stannius† added further cases in his Lehrbuch. It was, however, mainly owing to Wagner's lists that Duméril could give a general summary in Cuvier's posthumous edition of his 'Anatomie comparée,' published in 1836. Owen‡ also felt justified in summarising without referring any more to special cases. On p. 247 of his work he says:—"The symmetry [of the ovaria] is soon disturbed by concentration of development in the left ovarium, the right one remaining stationary, and ultimately, in most birds, disappearing." On p. 249: "Subsequently the left oviduct alone proceeds to grow; the right is stationary, or shrivels; occasionally it may be discovered as a rudiment in the mature bird, but usually all trace of it has disappeared."

Still further instances of abnormalities have been described and even figured without adding to or upsetting the generalisations quoted above. In most of the general text-books and others, which have occasion to mention these organs, the quotation of certain birds has become a regular stock in trade, always the same, copied from one author by the next, who in turn is quoted as the original authority by the more popular writer.

So far as I know, I was the first to give a possible explanation of the one-sided reduction, and I translate here what I wrote in Bronn's 'Thierreich,' p. 842, published in 1890. "In all birds only the left ovary is completely formed and functional; the right is present in most cases, and may even produce unripe eggs, but these degenerate later and seem never to become free. In correlation herewith the right oviduct undergoes early reduction; at most it persists towards the cloaca as a ligamentous strand, may be even as a tube which opens into the cloaca. This one-sided development of ovary and oviduct may be referable to saving of space. Two completely developed, hard-shelled eggs would scarcely have room in the belly, and we may add that even in the left oviduct two complete eggs seem to be very exceptional, if such ever occur. In Reptiles, however, both ovaries and ducts are equally developed."

This idea could not have been expressed more guardedly than by the following sentence in the 'Dictionary of Birds,' p. 783: "This one-sided suppression of the organs may possibly be

* Wagner: (1) Lehrbuch der vergleichenden Anatomie, 1834.
(2) Beiträge zur Anatomie der Vögel. Abhandl. Münch. Akad. Wiss. ii. 1837, pp. 271–283.

† Stannius's Lehrbuch der vergleichenden Anatomie. 1846.

‡ Owen: Anatomy of Vertebrates, vol. ii. 1866.

referable to the inconvenience that might be caused were each oviduct to contain an egg ready to be deposited." Mr. Gunn * takes a reporter's liberty by substituting for "inconvenience" various gruesome calamities, as fracture of the egg-shell, rupture of the oviduct, and even peritonitis! After thus having tried to throw ridicule upon my generally accepted notion, he assures us that such evil sequences need not be assumed at all because of "the frequency with which Falconidæ are found with paired ovaries, which are obviously functional." Then he proceeds to distinguish between several theoretical possibilities besides the only actual condition, namely, that in which the functional organs are those of the left side.

Not a single case is known of a completely developed right duct, whilst the left is vestigial. Further, I withdraw the statement made in the 'Dictionary of Birds,' that "but with rare exceptions only that [ovary] on the left side becomes functional." "Functional," I regret to say, was there used in a loose way, since the right ovary not unfrequently forms rather large eggs. But strictly it should be called functional only if any of those eggs ever became ripe, *i. e.* burst from the ovary. We know that even relatively large ovarial eggs, even those of the left side, can undergo complete reduction †.

Mr. Gunn, however, taking for granted that growing eggs in both ovaries mean that both are functional, and that, although two ovaries may not be a necessity, they must be better than one (a principle which has produced the double-barrelled gun), has to face the question whether one oviduct can serve two ovaries. We are told that "there is not much evidence for or against this supposition," and that "there seems no physical objection to the open end of the tube swinging across the mid-line of the spine, and grasping the right ovum of the opposite ovary with nearly the same facility as the ovum of its own side." One physical objection to this amazing trick-performance may be the gut with its loops and mesenteries, and it is at least doubtful whether the agile tube (the infundibulum of which is most carefully anchored opposite its own ovary) can overcome these obstacles, in spite of the best-intentioned regulating nerve-stimulus.

Let us enquire further into the meaning of the one-sided reduction of the female bird's reproductive organs.

Gegenbaur ‡ favours the size of the egg, the complete egg with albumen and shell, as the primary cause:—"Bei den Vögeln gelangt nur das linke Ovar zu seiner völligen Ausbildung dh. nur

* T. E. Gunn.—"On the Ovaries in certain British Birds," P. Z. S. 1912, p. 63. Mr. Gunn and the Rev. F. C. R. Jourdain credit the late Prof. Newton with the authorship of the article "Reproductive Organs" in the 'Dictionary of Birds,' and they suggest as his "German source" of original information Taschenberg's Introduction to Naumann's 'Naturgeschichte,' re-edited in 1905, eleven years *after* the 'Dictionary of Birds.'

† *Cf.* A. von Brunn: "Die Rückbildung nicht ausgestossener Eierstockseier bei Vögeln." Beiträge zur Anatomie und Embryologie, als Festgabe für Jakob Henle. Bonn, 1882.

‡ Vergleichende Anatomie der Wirbelthiere, ii. 1901, p. 503.

in ihm kommen Eier zur Reife, und das rechte erhält sich nur bei einzelnen (manchen Accipitres, Schwimmvögeln und einzelnen Gattungen verschiedener Abtheilungen) fort, indess es bei den übrigen verkümmert. Dies steht in Zusammenhang mit der Ausbildung nur eines (des linken) Oviductes und mit dem bedeutenderen Volum der Eier, wodurch jeweils nur einem einzigen ein längerer Aufenthalt in der engen Beckenhöhle gestattet ist. *Es ist also hier die Rückbildung einer Hälfte des gesammten weiblichen Geschlechtsapparates von der Ausbildung des Eivolums abhängig*, und dadurch an einen höheren Zustand geknüpft, dass das mit reichlichem Eiweiss und Dotter ausgestatte Ei das sich in ihm entwickelnde Junge zu einer bedeutenderen Ausbildung gelangen lässt." The correlations mentioned in these cumbrously involved sentences are valid enough, but they do not carry the question any further than where I had left it.

Since the ovary is the prime organ and the duct merely auxiliary, it might be assumed *a priori* that the primary cause of the reduction was the cessation of the production of ripe eggs on one side, whereupon degeneration of the corresponding duct would follow, as there would be no longer any work for it. Illicit, undesirable traffic is stopped best by cutting off the supply, in the present case by the stoppage of ripening eggs at the source. But, as we have seen, this does not agree with the facts, considering the frequent activity of right ovaries, whilst right ducts are much rarer. Further, we know that even comparatively far advanced ovarial eggs can be resorbed. Lastly, we should have every right to expect birds with right, and others with left functional organs. It cannot well be assumed that the one-sided reduction is an inheritance from reptilian ancestors, of which unfortunately we know nothing. Of recent reptiles only Crocodiles and Tortoises can be studied for the sake of analogy. These produce for one clutch a considerable number of hard-shelled eggs which pass through both ducts. The eggs are well protected, and there is ample room for them in the broad body of Chelonians, and there is likewise space and safety in the long belly of a Crocodile.

Presumably therefore the cause of the asymmetry should lie in the typical organisation of the bird. In proportion to its body the eggs are enormous, especially in some of the nidifugous groups which represent the lower conditions. They could not well produce the whole clutch at once; and they incubate their eggs, not merely because they require several days, even weeks, to produce the full number, but because as warm-blooded creatures they have reached a higher state of reproductive organisation. There is no room within the pelvis for more than one complete hard-shelled egg, leaving aside the inconvenience of a right and a left egg which, for argument's sake, might be overcome, as is actually the case with reptiles. The available space in the bird's belly is limited; the longitudinal distance is relatively much shorter than in the majority of reptiles which are devoid of a sacrum, and the peculiar pelvis of birds is as

broad as is compatible with the upright walking and with the flying organisation. Most likely the broadness and the absence of symphyses have been produced in adaptation to the eggs, but even the distention of the belly downwards must be limited in the bird, which is essentially and primarily a flying creature.

Well, then, let us take it that it is advantageous that one of the ducts and the activity of the corresponding ovary should be suppressed. Instances of asymmetry, brought about by suppression of one of originally paired organs, are common enough in the Vertebrata, and they can in most cases be fairly explained by mechanical factors. To refer them to mere accident, to a toss up, which then becomes established, is too shallow a mode, although not unprecedented in morphology. The tadpoles of some Anura have paired "spiracles," others a median, the majority a left hole. The reduction of one of the lungs of Snakes and snake-shaped Lizards is of course directly correlated with the shape of the body, and it appears almost optional whether the right or the left lung should be affected, since both cases have become established in the various groups.

If we apply the principle of elimination of all those unfortunate hen-birds which happened to produce eggs in either side, whilst only those birds propagate the race which happen to have only one side in working order, this would not explain the universal right-sided suppression, which according to Gegenbaur is a weighty argument for the monophyletic origin of the class *. If we assumed this as a proof of their monophylism, we should logically arrive not only at the imaginary pair of "Urvögel" but also at the Eve of hens, which in her case would relegate the establishment of the asymmetry to a toss up. During the presumably long period of dawning bird-life such a one-sided incipient suppression must have taken place over and over again before it was firmly established. Inheritance, if not swamped by panmixis, might have established asymmetry, but once more we are groping in the dark for a cause which favours the left side. It must be a factor which is very ancient and yet does not interfere with the symmetry of the male organs, neither the testes nor the vasa deferentia. Since the ovaries are strictly homologous, or rather homogeneous, with the testes, this may be taken as another hint that the ovaries are not the parts primarily affected. But the male ducts are not the same as the female ducts, therefore the latter are indicated. No factor causing the asymmetry can be derived from the vascular system, nor even from the vestiges of the renal portal system, by the suppression of which birds and mammals differ from their common ancestors, the reptiles. To refer the enlarged left ovary and duct to the

* The suppression of one lung in Snakes, etc. stands on a different footing. It may be due to an accident or sport, as much as right- and left-clawed crabs, or right- and left-twisted shells. The remaining lung enlarges and shifts its position so as to occupy most of the space originally intended for both.—H. G.

stronger arterial supply would of course mean mistaking effect for cause *.

A sufficient cause, however, may be the fact that a full oviduct is less liable to disturb the other intestines in the left half of the body-cavity than in the right. The primary intestinal loops are so arranged or packed, that their bases begin on the right whilst their apices extend towards or into the left side of the abdomen. This is especially the case with those loops which starting to the right of the stomach (itself mostly shoved to the left) fill the space between stomach and vent with their distal halves. It needs no further comment that it is the free or apical end, and not the base of a loop where the mesenteric vessels enter, which is displaced easiest and which will easiest resume its original position. But this packing from right to left is not an adaptation to, and is not produced by the preponderance of the left oviduct. It can be traced to a much more primitive condition, namely to the fact that the bird's embryo comes to rest with its left side upon the yolk, with its curved back towards the blunt pole. In all probability this is a truly cænogenetic feature, essentially ontogenetic; one of those numerous phenomena which, like the gills of tadpoles, the allantois and placenta, are originally incidental to embryonic life, although they may by correlated after-effects profoundly influence even the adult organism. Obvious results of this left-sided position of the embryo are the increasing preponderance of the left vitelline vein; the yolk-stalk causes the first loop of the midgut; the stomach itself sinks in, turning the pylorus to the right, upon which side the duodenal loop descends, and further secondary loops of the midgut follow suit. If there are large cæca, they likewise make their way towards the right and back of the stomach. The allantoic bag, containing fluid only, rises and comes to lie upon the embryo, *i. e.* upon its right side.

Consequently there is asymmetry introduced at an early date, which affects the viscera, notably the gut, and introduces a bias in their mutual behaviour within the belly. During the growth of the embryo, by shrinking of the yolk room becomes available for extension of the gut towards the left side. The permanent organs will soon—speaking from the point of evolution—establish an equilibrium, whilst it is clear that any occasional or contingent requirement of space, or disturbance, can be met with easiest in the left half. Such a disturbance is caused by the periodic growth and passage of the eggs which brook no delay. The slightest bias will turn the scales, and now we may apply the censorship of natural selection to its fullest extent. Left eggs

* The suppression of the right oviduct has had an effect upon the male copulatory organ. Where such is present it is asymmetrical, although unpaired, and stowed away in a left-sided recess of the cloaca. The act invariably takes place from the left side, and the same applies to those birds which are now devoid of such an intromittent organ.

and a left duct will be the least liable to set up complications. Two canals may be good, but one improved way is better, and if the traffic goes in one direction only, the other duct falls into abeyance. If goods are still produced at the terminus of the obsolete line, they will deteriorate, but this does not matter if the output of the opposite factory is equal to the demand.

So far so good, and the enquiry need not be carried further back, if it were not for the Monotremes. Although these archaic creatures show no appreciable difference in the size of their paired ovaries and ducts, only those of the left side are functional. According to Semon, *Ornithorhynchus* invariably produces two eggs, always in the left side; *Echidna* lays only one egg, also left-sided. The right ovary forms numerous large eggs which never ripen, and the respective duct and uterus are swollen and much vacuolised during the season. In short, Monotremes behave exactly like certain abnormal birds, *e.g.* the famous Sparrow-hawk, by the retention of an ancestral feature which is now normally lost. Since the reduction in the Monotremes has made so little progress, it looks as if it were but of comparatively recent date, but at the same time so ancient as not to have interfered with the inheritance of the full symmetry by the Meta- and Eutheria. The Monotremes are no longer quite primitive, not even in these organs. Their eggs have lost much of the yolk; they continue to grow in bulk within the uterus after they have received their keratine shell. Indeed, we cannot well imagine that, compared with oviparous reptiles and birds, the very small egg of the Monotremes, and the imperfect, almost larval condition of the new-born represent truly ancestral conditions, unless—and this is well worth further enquiry—we are prepared to assume that in all Vertebrata the viviparous condition was primary to one in which the fœtus is surrounded by a shell and then hatched outside the mother. If this should be the case, we should further have to distinguish between primordial viviparity (of which recent examples are unlikely) and secondary, pseudo-primitive viviparity, the numerous instances of which have been, and are still being, acquired independently: many Sharks and Teleosts; many Urodela, even one or two of the Anura, and many scattered cases among the reptiles, as some Chameleons and Lacertidæ, Iguanidæ and Anguidæ, all the Scincidæ, all the thoroughly aquatic snakes, the Viperidæ, and here and there some other terrestrial kinds. But to return to the Monotremes. Can their incipient, or perhaps arrested, asymmetry be referred to the same embryonic conditions as those which prevail in Birds? The bulk of the egg is formed by the yolk, the yolk-stalk might be strong enough to cause a disturbance, the allantois protrudes towards the right, and the left vitelline vein preponderates. How far, and if at all, the viscera are affected by these conditions, remains unknown. For our purpose it is significant that there is incipient asymmetry (functional although scarcely structural), and that this should be restricted to the only recent Mammals

which still possess comparatively large-yolked eggs. However, the Monotreme embryo does not turn upon its left side, it merely sinks into the cavity of the emptied yolk-sac, forming a proamnion; the bird, owing to its enormous yolk, turns over and ultimately comes to lie on its curved back; the reptilian embryo must also sink in, but it does not turn. This turning over, so marked a feature in the bird, may be correlated with the conditions of incubation. Everybody knows that the chalazæ keep the blastoderm "on the top," *i. e.* nearest the source of warmth, against the hen's body *. This does not apply to reptiles which deposit their eggs in the ground, nor to the one or two eggs in the moist pouch of the Monotremes; lastly, to the embryo of viviparous and ovoviviparous creatures "orientation" towards the source of heat is not only unnecessary, it would also be impossible because the mother changes so much her own position by moving about.

Since no trace of functional asymmetry of ovaries and ducts appears in Meta- and Eutheria, and as that of the Monotremes cannot well be a reptilian inheritance (because their asymmetry is usually marked by an enlargement of the right gonads and ducts, *e. g.* Snakes and Crocodiles, both sides however being functional), the asymmetry of the Monotremes must be due to a departure within the Prototheria, but so slight as not to have caused any irreparable morphological reduction of either ovaries or ducts by the time that the Prototheria entered upon the next higher or Metatherian stage, excepting of course the Monotremes. If Prototheria ever laid eggs much larger than they are now, the asymmetry may have been greater and be referable to the same primary causes as those suggested for birds, but since the recent Monotremes seem to be actually in the process of reducing them now, and moreover to the last possible number, the left-sidedness seems to be a case of mere coincidence with birds.

Some simplification of the completely double female apparatus of the Vertebrates was bound to come; it was a matter of time, and success depended upon the grade or height of the general organisation of those who attempted it. Any agreement between birds and mammals versus reptiles cannot be anything more than convergent resemblances, at best cases of Isotely. The classes of both Birds and Mammals have gone beyond the level of the Reptilian organisation and they represent highest termini; but, although the class of Birds is by far the most specialised and in various respects has reached seemingly unsurpassable perfection, the class of Mammals is morphologically the highest, in spite of its still comprising such lowly, undecided types as the

* The usual statement that the hen turns the eggs over from time to time in order to ensure the equal warming of the whole egg, now the upper and then the lower half, implies nonsense. What the sitting bird does, is to rearrange the position of the eggs with reference to each other, to give those now lying peripherally an equal chance of best position near the centre. With a small clutch this is not necessary, but with a dozen eggs the frequent rearrangement is very noticeable, at least with thoughtful sitters.

Monotremes (*cf.* loss of the nucleus of red blood corpuscles, structure of the atrio-ventricular valves, the alveolar lungs, the abolishment of the cloaca, the cranio-dental articulation of the underjaw, etc.).

The Elasmobranchs show various instances of precocious inventions, ahead of the times, foredoomed to failure or further improvement, because their owners are after all but low fishes. In some the ovary is single, unpaired, but it lies in the middle. Some Acanthopteri have succeeded in producing a median duct out of their otherwise paired ovarial sacs. Birds, as we have seen, have suppressed one side; a clumsy mode of procedure because it has a lopsided result and implies the reduction, by neglect, of one of the precious gonads. It is only the higher-graded organisation of the Mammals which has succeeded in simplifying the apparatus in the morphologically neatest way, namely, by the partial fusion of the two ducts into one passage, not only unpaired, but median, whilst the upper ends and the ovaries remain intact and functional.

Monotremes, Marsupials, and Placentals form an unbroken, progressive, therefore most probably monophyletic series. The reduction in question could not be brought about until the reptilian plan of hard-shelled eggs had given way to internal gestation. The differences between oviparous, ovoviviparous, implacentally and placentally viviparous, are questions of degree only. There is for instance no difference, to be expressed in a few words, between the ovoviviparous fruit of a Viper and the newborn fœtus of a Kangaroo, except that the newborn reptile is complete and must shift for itself. The point is that the young bursts its egg, and other membranes, with the act of birth. Whilst no newborn reptile requires maternal care, most birds do, and all mammals are absolutely dependent on their mothers for nourishment.

Within the Class of Birds every stage from almost reptilian to practically mammalian conditions is represented. The typical nidifugous birds are hatched with still a considerable amount of yolk slipped into the belly, sufficient for the little ones to hold out for days without food until they are bodily and mentally strong enough to feed themselves; in many cases they have to be shown by the parents how to do it. Next come those which are hatched in a more or less helpless condition and must be fed by the parents with food either in its natural state or already semidigested. Lastly, those which are nursed with a milky secretion of the crop. The higher Altrices or Nidicolæ are born with but small remnants of yolk left, the digestive organs having been hurried on at the expense of the others. The most significant point, however, is that through the crop-secretion the Pigeons have established a parallel with the Mammals in so far as the young are fed actually with parental matter, in which proliferation and fatty degeneration of epithelial cells plays a great part. The analogy can be carried still further, since by

Pigeons and some of the lower mammals this "milk" is squeezed or injected into the young.

The Mammalian evolution has probably gone through many stages and vicissitudes, difficult to enumerate, because there were many factors and not all the organs changed at the same time.

1. We start with a hypothetical stage of Sauro-mammalia. The hard-shelled egg, when laid, contains an already far advanced embryo, therefore ovoviviparous. This egg was not so much incubated for warmth as covered for protection by the mother. The young although hatched in a reptilian condition was protected by the mother.

2. Reduction of the size of the egg. Gradual preponderance of extra-uterine nursing over uterine gestation, made possible and introduced by the protecting insulation, in such a way that an abdominal incubation area was developed, owing to the reaction of the mother's abdominal surface by the sat-upon, adpressed, covered egg; this resulted in hypertrophic condition of the cutaneous blood-vessels, hence of the glands, and correlated reduction of hairs. Incidental change of absorption of moisture through the porous shell, enhanced by loss of its calcareous portion.—When this suppression had been well established, by progressive inheritance, the now quite porous parchment egg had the same chances of absorbing fluid whilst still in the oviduct. At the same time it stands to reason that the chances of external or brood-pouch nourishing may become prevalent. The shortening of the life-period within the egg implies the birth of an unripe fœtus. Fœtal life must be taken as ending with the bursting of the egg, no matter whether this act coincides with the moment of parturition, or whether it happens some time after the egg has been "laid." In either case it coincides with the cessation of any further possibility of function of yolk-sac and allantois.

We must further assume that the actual length of time required for the production of a young animal is the same in equal-sized creatures from the beginning of segmentation until it is independent. Unless we assume this, the argumentation would become too complicated.

Let us say that it took 50 days from impregnation until the Sauro-mammalian youngster was ready to face the Permian world. This means:

50 days of ovoviviparous, internal uterine life								(Sauro-mammal).
40 days uterine and 10 days incubation-life within the laid egg								(Hypotheria).
30	„	„	10	„	„	and 10 days nursing in pouch		(Prototheria).
20	„	„	5 ?	„	„	25	„ „	(Monotremes).
8	„	„	0	„	„	42	„ „	(Opossum).

The suppression of the incubation-life marks the Metatherian stage just as sharply as the introduction of incubation of a fœtus marked the early Mammal stage. The adaptation to the

new invention of pouch-life and nursing caused the development of an entirely new category of features—of features which were not required either by the fœtus or the adult, therefore *larval*, *e. g.* a suctorial apparatus with its far-reaching incidental influences upon the future adult structures.

In these respects viviparous reptiles, Hypo- and Prototheria culminating in Monotremes, and Metatheria culminating in Marsupials, represent a continuous progressive series, with a logical terminus characterised by the enormous preponderance of extra- over intra-uterine development. Compared with these terminal Marsupials the Eutheria seem to be totally different, provided we take as their type those which are born complete, in this respect like the hypothetical Sauro-mammals, the whole of the "50 days" being intra-uterine. And yet the Eutheria have with certainty passed through the same Metatherian stage as have the Marsupials, and this Metatherian stage comprised, besides others, the following features*: Truly viviparous; allantoic placenta; marsupium; diphyodont teeth, the same two middle series of a total of prelacteal, lacteal, permanent and post-permanent sets; nipples; semi-cloaca; absence of a corpus callosum.

To arrange any one of these features into successive morphological stages is comparatively easy, but it does not follow that these represent exactly the phylogeny of the groups, because of the complicated correlations with other organs which by no means keep step with each other, neither in the same species nor in the greater groups. Some are precocious, even hypertelic, while others lag behind.

Just as to the large egg of the truly oviparous Sauropsids albumen (more watery but less fatty yolk) is added, before it receives its calcareous shell, so in the Monotremes fluid is added to the contents of the egg, but with the remarkable difference that fluid matter is taken into the yolk-sac itself by osmosis from the uterine walls, *after* the keratine shell has already been developed. This process is correlated with an undoubted previously acquired reduction of the amount of ovarial yolk, and is as much a secondary process as the loss of calcareous matter in the parchment-like "keratine" shell.

As Semon has shown, the whole shell-enclosed egg multiplies its size during its passage through the oviduct. This mode of growth finds a curious parallel analogy in various Lacertilia, the parchment-shelled eggs of which grow considerably after they have been deposited.

Whilst the Sauropsidan allantois comes to surround the whole yolk-sac and also nearly the whole of the albumen, so as to spread over most of the inner surface of the egg, the Monotreme

* *Cf.* R. Semon: "Monotremen u. Marsupialier," in Zoolog. Forschung. Australien, ii. 1894–97; further, J. T. Wilson and J. P. Hill's papers in Q. J. M. S. 1897, 1898, 1900.

allantois and yolk-sac balance each other. The shell-enclosed egg is for a short time transferred into the marsupium (*cf.* Semon, Echidna; not into a bursa as was imagined by Klaatsch, Gegenbaur, and others), which secretes fluid (the "nutritive sweat" in Gegenbaur's unfortunate diction), and this can be taken up by the embryo through the porous shell. This may be the reason why the shell is soon cast off.

In Marsupials the shell is at first still present, but soon absorbed within the oviduct. The egg-membranes, etc., of the embryo establish no structural communication with the uterus. The ovarial yolk is much reduced. But the yolk-sac becomes enlarged, as in the Monotremes, still occupies a great portion of the inner egg-surface, and has established intimate contact with the serosa. The allantois, being independent of the expansion of the cœlom, which results in the driving away of the yolk-sac vessels from the somatopleure, establishes a villous placenta. Such must have been the condition of the Metatheria.

In *Perameles* the allantois still reaches the surface, where it is very vascular, and fused with the serosa, a truly respiratory arrangement. The placenta being lost in most other Marsupials, the allantois reverts to its primary function of urinary receptacle, although apparently late during the fœtal life.

The Metatherian stage may therefore be characterised as one in which the posterior of the two bags, the allantois, has superseded the previous attempts of placentation by the yolk-sac. The new placenta was perhaps not advanced enough to prevent the fœtus from being born soon after the limited amount of yolk was used up. Certainly it did not pass beyond the non-deciduous stage, and it never reached the extent of even the lowest recent Eutherian placenta. Yet one effect of this incipient organ must have been to render the fœtus less independent than that of a viviparous reptile. It had therefore still to be transferred into the marsupium, there to be kept moist and suckled in as premature a condition as the Monotreme.

Two opposite tendencies are inherent to this stage. One palingenetic, to give birth when the yolk is used up; the other cænogenetic, to prolong the retention of the fœtus because of the compensatory, respiratory, etc. advantages incidental with a placenta. Obviously the Metatherian stage was a half-way house at a parting of the ways to further improvements, leading to Marsupials* and to Placentals.

* We have here an instance of the well-known fact that Group-names based upon single anatomical features are mostly unsuitable for classificatory purposes. The taxonomic value of these characters may be good enough, but they are not diagnostic. If such names were used merely as labels without much intrinsic meaning, well and good, but even the best of us cannot, on occasion, resist taking their face-value for full value. There are Mammalia Implacentalia with a placenta, and we now know that the young Echidna does not lie in a bursa. Odontornithes are a valueless, heterogeneous assembly, and overconfidence in "Ratitæ" was responsible for having branded *Hesperornis* as a "swimming Ostrich." "Mammalia" is fortunately an excellent term, although invented before Monotremes were known.

To judge from analogy the new organ should continue straight on, leading in this case through a diffuse and cotyledonary to a solid, and from a non-deciduous to a deciduous placenta, terminating in the birth of the young in an utterly helpless condition. As a rule the non-deciduous and diffuse placenta is found in those mammals which at birth require least maternal care. The latter implies greater mental capacity. But we also know from analogy that a recent invention—although it may be capable of much perfection—is not always kept up if the old string to the bow is still capable of further adaptation. Where both alternatives are good, workable, and capable of being improved, it may take a long time to settle which is after all the better of the two.

What has induced some Metatheria to neglect the further development of their placenta and to intensify the marsupial alternative? The morphological and physiological momentum was surely on the side of improving placentation. There must have been some external, environmental influence, and it was Dollo's brilliant suggestion that arboreal life was the underlying cause. His further explanation is less acceptable, that the climbing habits have caused premature births, which have become habitual, and that the hapless fœtus had therefore to be nursed and located in a marsupium, the bursa, or rather multiple bursæ, being no longer sufficient.

I think the new conditions to be faced by intense arboreal life have acted somewhat differently, especially if, as we assume now, all the Metatheria were already possessed of a marsupium*.

I venture to suggest that those Metatheria which were driven to arboreal life, had to solve the question what to do with their young. They had to carry them, and being already possessed of the pouch, this was not only retained but intensified by prolonged use. That the facilities offered by such a pouch are great, is shown by the still existing numerous and much diversified Marsupials, and by the fact that some at least, *e. g.* Opossum, have reduced the uterine gestation almost to the conceivably lowest limit. Whilst these arborealised Metatheria could not afford to leave their young behind, it was different with those other Metatheria which during the Cretaceous epoch somewhere "in the larger and more effective workshops of the North" (to apply here one of Darwin's happiest expressions) went

* Klaatsch's view of the correlation between Bursæ and Marsupium had to be considerably modified by Semon's discovery that the Monotreme does not lie in a bursa but in an already typical, though transient, marsupium. Moreover, there are unmistakable vestiges of marsupial muscles, other than compressores mammæ, in various Placentals. Lastly, each teat with its areola does represent a bursa (Klaatsch), but if each bursa had been a brood-pouch instead of merely the result of the attachment of young, the possession of a series of bursæ from near the vulva up to the armpit would imply an impossible condition. In fact, bursæ or nipples can be formed independent of a marsupium and in places whereto no such organ can have extended.

in for that further mental development which is intimately correlated with the origin of the corpus callosum. Competition is most effective if backed by brain-power. Where these dawning Eutheria spread the other Metatheria had to go to the wall, or were forced to get out of reach—into the trees. Those which, already arborealised, found their way into countries like Australia, where the Eutheria could not follow in time, found there nothing to prevent them from becoming again terrestrial, as Dollo has shown so conclusively. The chance of reviving the degenerated placenta was, however, gone, and the Marsupials are now, in spite of the retention of various low characters, the most specialised subclass of Mammals.

The Edentates present a striking analogous case: being without exception arboreal or fossorial, they also seem to have got out of the way of mentally higher, dangerous Eutheria. They have survived, whilst those that went in for heavy bulk and armour were not a great success. At least the American Edentates seem to have come into contact with the dangerous Eutheria long after they themselves had become typical Eutheria, so that the former possession of a marsupium could avail them nothing.

A few words about the Eutheria. They could afford to part with their young for a time and to suckle them intermittently, an advantage which needs no further comment than that it would be impossible without higher mental faculties.

Great adaptive changes have been wrought; every chance has been tried, now here, then there. Nearly all the Non-deciduata are at birth precocious, able to look after themselves, no matter whether the placenta is diffuse, cotyledonary or zonary even, namely the aquatic Cetacea and Sirenia, and the Artio- and Perissodactyles, the exception being the Lemurs. The Deciduata are at birth helpless: Rodents, Insectivores, Carnivores, Chiroptera, Tarsius and Simiæ, except the Elephants.

The egg-laying Monotremes, the implacental Marsupials, and the Mammals with the most advanced placenta, are born in a condition as helpless as the highest nidicolous birds, whilst the avowedly low non-deciduous and diffuse placenta of the Mare i sufficient to produce a young which is as precocious and independent as a lizard.

Can these facts be brought into line? What is here primitive and what is a roundabout return to apparent but not really ancestral conditions?